Clustered or scattered? The impact of habitat fragmentation on establishment and early spread

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Title

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Abstract

Habitat quality is a major predictor of establishment success for an introduced species. Yet, introduction areas are usually landscapes, i.e. heterogeneous sets of habitats that are more or less favourable to the introduced species. As individuals are likely to disperse as soon as they are introduced, the quality of the habitat surrounding the introduction site is as critical to the persistence of introduced populations as the quality of the introduction site itself. Moreover, demographic mechanisms such as Allee effects or dispersal mortality can also hamper dispersal and affect spread across the landscape, in interaction with the spatial distribution of favourable habitat patches. In this study, we investigate the impact of fragmentation, defined as the degree of scattering of a constant amount of favourable habitat, on establishment and early spread. First, we simulated introductions in one-dimensional landscapes for different dispersal rates and either dispersal mortality or Allee effects. The landscapes differed by the fragmentation of favourable habitats, which were either “clustered” into few large aggregates or “scattered” into multiple smaller ones. Second, we tested the predictions of simulations by performing experimental introductions of hymenopteran parasitoids (*Trichogramma chilonis*) in "clustered" and "scattered" microcosm landscapes. Results highlighted two impacts of fragmentation. By increasing the risks of dispersal from the introduction site to unfavourable habitat early during the invasion, fragmentation decreased establishment success. However, by decreasing the distance between favourable habitat patches, it also improved the subsequent spread of introduced species over larger areas.

Introduction

Establishment is a crucial phase of biological invasions, which determines whether the introduced populations turn into self-sustaining colonies likely to spread or go extinct (Blackburn et al. 2011). The match between the characteristics of the introduced species and

the environmental conditions they experience in their new habitat is a major predictor of establishment success (Shea and Chesson 2002, Moles et al. 2008). Yet, introduction areas are usually natural landscapes, made up of habitats of different quality (Turner et al. 2001). Establishment can be affected by the heterogeneity of the introduction area (Melbourne et al. 2007), as well as the spatial distribution of these habitats of different quality (Schreiber and Lloyd-Smith 2009). This study focuses on the impact of habitat distribution in terms of fragmentation. The denomination of "fragmentation" is widely used, to convey different meanings depending on the context. Following Fahrig (Fahrig 2003), we consider it here as the scattering of favourable habitat without habitat loss. Therefore, it describes a particular structure of habitat distribution at the landscape scale: a given amount of favourable habitat will be broken apart in fragmented landscape but aggregated into large clusters in a non-fragmented one (McGarigal and Cushman 2002, With 2002).

The impact of fragmentation on invasion success is linked to colonisation, which is not only essential for spread, but also for establishment. Introduced populations are known to have high extinction risks because of their small initial size (Simberloff 2009), and emigrations from the introduction site will slow down their growth, thus increasing this risk further (Kean and Barlow 2000, Parlato and Armstrong 2013). Dispersal can nevertheless be beneficial as it allows the creation of new colonies, and increase overall persistence in the long run (Morel-Journel et al. 2016). These effects of dispersal on establishment are tightly linked to the spatial structure of the introduction area, and in particular its level of fragmentation. Simulation results by Schreiber and Lloyd-Smith (2009) indicate that individuals introduced in favourable habitat have higher chances of dispersing to less favourable habitat if the landscape is fragmented. Dispersing individuals are then less likely to colonize new habitat patches. In less fragmented landscapes, a favourable introduction site is more likely to be in a larger cluster of favourable habitat patches (Schreiber and Lloyd-Smith 2009), and thus safer for emigrating individuals.

However, fragmentation can also facilitate early colonisation across larger spatial scales, as the breaking apart of habitat tends to reduce the mean distance between the patches of favourable habitat (Fahrig 2003, Roques and Chekroun 2010). It therefore increases the probability of successfully dispersing to those habitats, and form new colonies. In a theoretical study, Dewhirst and Lutscher (2009) thus indicate that aggregating resource into larger and more isolated clusters can prevent spread. It is therefore possible to identify two spatial scales at which fragmentation has two different impacts: decreasing persistence of populations in the direct surroundings of the introduction site, and increasing colonisation in the rest of the landscape.

These opposite effects of fragmentation on dispersal will likely be affected by demographic processes that shape colonization dynamics in heterogeneous environments. Mechanisms such as dispersal mortality or Allee effects create additional costs to dispersal that make colonisation more difficult. Dispersal mortality eliminates dispersing individuals, thus reducing the chances that some of them reach favourable habitat to colonise. On the other hand, Allee effects can bring small populations to extinction at low densities (Allee 1949, Courchamp et al. 2008), and prevent colonisation if the number of individuals dispersing to a new patch is too low (Keitt et al. 2001). By affecting colonisation success these mechanisms are susceptible to exacerbate the effects of fragmentation.

Although fragmentation has been identified theoretically as a key element of landscape structure as regards to the dynamics of expanding invasive populations, experimental confirmations of the impact of resource distribution on the establishment and spread of introduced populations remain scarce. This study aims at bridging this gap between theory and empirical data by investigating the role of fragmentation with both simulations and experimental results. First, we developed a simple model describing a biological invasion in a spatially explicit context. We designed heterogeneous one-dimensional landscapes with

alternating “bad” and “good” patches, according to their quality, and centred around the introduction site. Two fragmentation levels were considered: “scattered” landscapes (high fragmentation level) alternated one good one bad patch, and “clustered” landscapes (low fragmentation level) alternated three good and three bad patches (Figure 1A, B). We simulated invasions in these landscapes for different dispersal rates, combined with either dispersal mortality or Allee effects. Then, we tested the predictions from the model by monitoring artificial introductions of the hymenopteran parasitoid *Trichogramma chilonis* in artificial landscapes with the same structure, with two levels of fragmentation and dispersal mortality.

Methods

Structure of the landscape

The heterogeneity studied in the introduction area was created with two kinds of patches with different resource levels: “bad” patches with a low carrying capacity (K_1) and good patches with high carrying capacity (K_2). The difference between the two patches qualities was set to $K_2 = 5K_1$, to ensure significant differences between the two treatments. Those patches were arranged as a linear chain according to a one-dimensional stepping stone model (Figure 1A, B). Fragmentation was created by alternating good and bad patches along the spatial axis: scattered landscapes alternated one good one bad patch, while clustered landscapes alternated three good and three bad patches. Although the pattern could theoretically repeat infinitely, we focused here on establishment and early dispersal, occurring in the surroundings of the introduction site only. Therefore, our landscapes were made up of eleven patches (five good and six bad), with the introduction site (a good patch) in the centre. Those landscapes structures were used for the simulations as well as the experiments.

Model and simulations

The model used here is adapted from Morel-Journel et al. (2016) and describes the dynamics of a population in a one-dimensional stepping-stone landscape *W*. This model aims at describing general population dynamics and bringing insight on invasion dynamics regardless of the species considered.

$$N_{i,t+1} = f\left(\sum_{j \in W} M(i,j) N_{j,t}\right), \quad (1)$$

with $N_{i,t}$ the population size at generation *t* and location *i* in the landscape *W*. The value of $N_{i,t}$ is systematically truncated to the nearest integer and the population is considered extinct for $N_{i,t} < 1$. This model comprises two successive phases: (i) a dispersal phase associated with the dispersal kernel *M* (*i*, *j*) describing the probability that an individual disperses from locations *j* to *i* and (ii) a growth phase, with *f(.)* a function describing the growth of the population at location *i* after dispersal.

At each dispersal phase, the probability that an individual disperses from patch *j* to patch *i* thus depends on their distance:

$$M(i,j) = \begin{cases} 1 - 2d_{j,t}, & |i-j| = 0 \\ (1-m)d_{j,t} & |i-j| = 1 \\ 0, & |i-j| = 2 \end{cases}, \quad (2)$$

where $d_{j,t}$ is the probability that an individual disperses to one of the neighbouring patches and *m* accounts for dispersal mortality. Individuals can only stay in their own patch ($|j-i| = 0$), or disperse to an adjacent patch ($|j-i| = 1$). This limited kernel allows us to focus on short-distance dispersal, and corresponds to the dispersal behaviour also observed in the experimental setup used conjointly with the simulations. The growth phase is described by a Ricker model including an Allee effect (Courchamp et al. 1999, Brassil 2001):

$$f(x) = xe^{r\left(1-\frac{x}{K}\right)\left(1-\frac{A}{x}\right)}, \quad (3)$$

when $x \geq 1$ and $f(0) = 0$. Here *r* is the per capita growth rate and *A* is the Allee threshold. There is no Allee effect when $A = 0$, a weak Allee effect when $0 < A < 1$ and a strong Allee effect when $A > 1$. We added a normally distributed noise ε to the deterministic growth rate in (3) to

take demographic and environmental stochasticities into account (Lande et al. 2003):

$$f(x) = xe^{r\left(1-\frac{x}{K}\right)\left(1-\frac{A}{x}\right)+\varepsilon},\ \varepsilon \sim N\left(0, (\sigma^2, \sigma_e^2 + \frac{\sigma_d^2}{x})\right). \quad (4)$$

σ^2_e and $\frac{\sigma_d^2}{x}$ correspond to variability in the population growth rate respectively caused by environmental and demographic stochasticity. As demographic stochasticity stemmed from the variability in individual fitness, its effect on the population growth rate was averaged over the whole population: if the variance in individual fitness from one individual to the other was the resulting variance at the population scale was $\frac{\sigma_d^2}{x}$.

The model was used to simulate introductions the landscape described in the previous section, for K_1 = 60, so that populations around carrying capacity would be safe from potential Allee effects, and K_2 = 300 to maintain the 1:5 ratio between K_1 and K_2. We followed the invasions during 10 generations, for different values of dispersal rate ($d_{j,t}$ varying between 0 and 0.4) and a mechanism adding a cost to colonisation : either an Allee effect (A varying between 0 and 10) or dispersal mortality (m varying between 0 and 1). Because the model is stochastic, each combination of parameters was simulated 1000 times for r = 1, σ^2_e = 0.1 and σ^2_d = 0.1. For each simulation, the maximal extent of the metapopulation was computed as the number of good patches colonized outside of the introduction site.

Experiment

In complement of the simulations, we performed introductions of the parasitoid wasps *Trichogramma chilonis* (*Hymenoptera: Trichogrammatidae*) in artificial landscapes with the structures described previously, and monitored the dynamics over ten generations. Each generation lasted nine days, including two days of adult life, after which the adults were manually removed from the experiment to maintain non-overlapping generations. During their adult life, individuals were able to move freely between patches by going through corridors.

According to previous experiments in similar conditions (Morel-Journel et al. 2016), they were expected to disperse at most from one patch to an adjacent one during their adult life. Resource was provided in the form of eggs of the Mediterranean flour moth *Ephestia kuehniella* (*Lepidoptera: Pyralidae*) for *T. chilonis* to parasitize. As only one individual is usually able to fully develop from one host (Suzuki et al. 1984), the carrying capacities in the experiment were controlled by the number of hosts available. Good patches were provided with approx. 450 eggs at each generation, as previous experiments by Vercken et al. (2013) indicate that *T.chilonis* populations would reach carrying capacities around 300 individuals in these conditions. The bad patches were provided with approx. 90 eggs to maintain the 1:5 ratio between K_1 and K_2. The larvae developing within *E. kuehniella* eggs would eventually turn dark because of the chitinisation of the parasitoid pupae (Reay-Jones et al. 2006). Parasitized eggs were then counted on photograph with the ImageJ software (Rasband 1997) and their number was considered a reliable proxy of the number of adults in the next generation. Data obtained through the monitoring of parasitized eggs counts were subsequently analysed with the R software (R Core Team 2015).

We set up a 2 x 3 factorial design for the experiment, with the two fragmentation levels (scattered and clustered) and three levels of dispersal mortality. All the combinations were replicated in twelve experimental blocks, for a total of 72 experimental introductions. We only considered one type of cost to dispersal to increase the number of experimental replicates and have more statistical power in the analyses. Dispersal mortality was chosen over a demographic Allee effects, which is more species-dependent and less widespread in empirical data (Kramer et al. 2009, Gregory et al. 2010), despite a large use in theoretical studies. We were able to manipulate dispersal mortality by adding optional dead-end exits to the pipes connecting adjacent patches. Those dead-ends made successful dispersal to neighbouring patch less likely, as individuals stayed in these dead ends without finding the next patch (results not shown). Two

adjacent patches were thus connected with either (i) two regular pipes for low dispersal mortality, (ii) one regular and one pipe with a dead-end exit for medium dispersal mortality, (iii) two pipes with dead-end exits for high dispersal mortality (Figure 1C, D, E).

To accurately characterise the impact of heterogeneity itself in the landscape, we computed the extinction rates of good and bad patches (as the number of extinctions over the number of colonisations for each replicate), and compared them using a paired Wilcoxon test. As we expected to observe different effects of fragmentation on early invasion at two different spatial scales, we characterized (i) the surroundings of the introduction site as the two good patches closest to the introduction site and (ii) in the rest of the landscape as the two good patches furthest from the introduction site. We computed the surroundings and landscape occupancy rates as the proportion of replicates in which at least one good patch was colonised, in the surroundings and the rest of the landscape respectively. The surroundings occupancy rate was analysed with a binomial general linear mixed model, the experimental block as a random effect. Model averaging was over the candidate models according to their AIC_C (Grueber et al. 2011): (i) without any fixed factor, (ii) with dispersal mortality as a factor, (iii) with landscape fragmentation as a factor, (iv) with the additive effect of both factors (Supplementary Material). As there were very few colonisations in the rest of the landscape, the landscape occupancy rate was analysed with Fisher's exact tests.

Results

In accordance with our predictions, we observed an overall positive relationship between colonisation and the dispersal rate, and a negative relationship between colonisation and the mechanism creating additional costs to colonisation, i.e. Allee effects or dispersal mortality (Figure 2). The impacts of the two mechanisms on colonisation were similar. By comparing colonisation rates in scattered and clustered landscapes, we evidenced parameter

combinations for which colonisation was affected by the fragmentation level. For high colonisation costs and very low dispersal rates, populations in clustered landscapes performed better than those in scattered landscapes: the first managed to colonise the surroundings of the introduction site, i.e. the three patches of local cluster while the second only colonised the introduction site. In contrast, for intermediate dispersal rates and low colonisation costs, populations in clustered landscapes achieved lower colonization than those in scattered landscapes: the first only colonised the surroundings of the introduction site while the others managed to colonise the rest of the landscape.

Experimental results confirmed the impact of habitat quality on local population dynamics, as the bad patches had a significantly higher extinction rate than the good ones (paired Wilcoxon test, $V = 706.5$, $p < 0.001$). We also observed clear patterns concerning the colonisation (Figure 3). We assessed the occupancy rate of the good patches surrounding the introduction site, and in the rest of the landscape separately. The fragmentation level affected negatively the surroundings occupancy rate (Wald test, $z = 4.282$, $p < 0.001$), but positively the landscape occupancy rate (Fisher's exact test, $p = 0.025$). Thus, populations introduced in clustered landscapes managed to colonise the patches surrounding the introduction site more often than those in scattered landscapes, but did not manage to successfully colonise the good patches outside of their local cluster. Finally, we evidenced a negative impact of dispersal mortality on the surroundings occupancy rate (Wald test, $z = -2.243$, $p = 0.025$), but not on the landscape occupancy rate (Fisher's exact test, $p = 0. 865$).

Discussion

Simulation and experiment results confirm the twofold impact of the fragmentation level of the landscape on invasion success, depending on the costs associated with dispersal. Breaking apart a constant amount of favourable habitat in small fragments in the landscape

reduced the formation of colonies close to the introduction site, while facilitating dispersal over larger scales. When colonisation was not impaired (when the costs of dispersal were low or inexistent), simulation results indicated that fragmentation could facilitate colonisation at larger scales by reducing the maximal distance between good habitat patches. These results were consistent with the patterns observed during the experiment. Indeed, the only recorded colonisations of the furthest patches from the introduction site occurred in scattered landscapes. They also concur with earlier theoretical work on the positive effect of fragmentation on invasive spread (With 2002, Fahrig 2003). Indeed, fragmentation can provide stepping stones, which increase connectivity within a landscape (Schippers et al. 2008, Saura et al. 2014). When the costs associated with dispersal were higher, the impact of fragmentation became deleterious to colonisation. Dispersal mortality and Allee effects increased the minimal number of dispersing individuals necessary to successfully colonise patches, respectively by eliminating some of them during dispersal and by raising the minimal initial population size necessary to ensure colonisation. The presence of bad patches, harbouring fewer individuals, around the introduction site in scattered landscapes, did not prevent colonisation of other good patches altogether, although it made it more difficult. This conclusion is supported by the lower colonisation rate of the surroundings of the introduction site observed during the experiments in the scattered landscapes.

In previous studies on the subject, bad patches were characterized by a negative population growth rate (Lutscher et al. 2006, e.g. Dewhirst and Lutscher 2009) and so acted like barriers to dispersal. In our study, heterogeneity was created by the carrying capacity. Therefore, they could harbour populations, although smaller than those in good patches, and much more prone to stochasticity. Indeed, results show that the local extinction rate was much higher in bad patches, and an additional logistic regression over patch extinction during the experiment showed a negative correlation between population size and extinction probability

261 ($z = -6.913$, $p < 0.001$). This positive relationship with time before extinction proposed by
262 Lande (1993) effectively links the carrying capacity to habitat quality. Because of this
263 instability, bad patches acted more as stepping stones between the good patches than habitats
264 harbouring persistent populations. Moreover, the small size of the populations in bad patches
265 made dispersal between the good ones more difficult. Indeed, small populations are less likely
266 to produce enough successful dispersing individuals to colonise other patches (Morel-Journel
267 et al. 2016). This is also confirmed experimentally, as another logistic regression showed that
268 empty patches had higher chances of being colonised when they were next larger populations
269 ($z = 3.796$, $p < 0.001$). Although the scale of fragmentation we used in this study did not prevent
270 dispersal between good patches altogether, it made it more challenging.

271 Several theoretical studies underline the importance of the scale of the fragmentation
272 of the landscape. It has to be in the same order of magnitude as the dispersal capabilities of
273 individuals to impact the invasion process (With and King 1999, With 2002, Dewhirst and
274 Lutscher 2009). Indeed, the presence of unfavourable habitat is not relevant for individuals that
275 can always easily disperse between good patches. Thus, Dewhirst and Lutscher (2009) argue
276 that fragmentation should be considered relative to individual dispersal patterns. Previous
277 experiments by Morel-Journel et al. (2016) in a similar experimental context indicate that
278 *Trichogramma* were at most able to colonise patches directly adjacent to existing populations.
279 Similarly, in our simulations, individual dispersal during a generation was limited to the
280 neighbouring patch. Therefore, individuals were not able to avoid the bad patches altogether,
281 although they were still able to get through them by forming small, unstable colonies in the bad
282 patches. Adding long distance dispersal events could modify the impact of fragmentation on
283 colonisation, as they can drastically change spread patterns across space (Johnson et al. 2006,
284 Fletcher and Westcott 2013).

285 The focus of our study – the initial establishment of an introduced population and the

colonisation of nearby patches – conditioned the size of the landscape studied. Indeed, we chose to consider a landscape of limited size (eleven patches), which represent a section of an infinite landscape with alternating good and bad patches. Similar one-dimensional landscapes have been used by Shigesada et al. (1986) and Dewhirst and Lutscher (2009) to model the effects of fragmentation on colonisation. Despite its small size, the landscape we focus on allowed us to observe two distinct colonisation patterns in clustered landscapes: within a cluster and between clusters. The first one is much easier than colonisation in fragmented landscapes, and occurs even when colonisation costs are high. However, the second is more difficult and can drastically limit the spread of individuals. Over larger scales, the spread pattern is therefore expected to alternate between rapid colonisation of clusters, followed by much slower colonisations until invaders manage to reach the next cluster. In landscapes with very low fragmentation levels, the stagnation time could become overwhelming, thus effectively circumventing the invasion to the clusters already colonised. This could be the case of our experimental results in clustered landscapes, although the time to reach a new patch could also be greater than the duration of the experiment. Other theoretical studies suggest that the dual effect of fragmentation we demonstrated on one-dimensional theoretical and laboratory landscapes should persist un higher dimension (With and King 1999, Roques and Chekroun 2010).

The effects of fragmentation, with or without habitat loss, on the dynamics of already established populations, has been largely documented through empirical studies in the context of conservation (Haddad et al. 2015). However in invasion biology, the subject has been mostly addressed by theoretical studies, although the usage of fragmentation as a tool for the management of invasion has been proposed in the past (Novinger and Rahel 2003, Alofs and Fowler 2010). Our results indicate that habitat fragmentation could indeed isolate introduced populations, but that it can also promote spread over larger scales. However, the outcome of invasions in scattered and clustered landscapes is also highly dependent on the costs associated

to colonisation, either the mortality during dispersal, or the failure to reproduce after dispersal because of Allee effects. This study confirms that considering the spatial distribution of favourable habitat across the introduction area, and especially its interaction with population dynamics is critical to assess establishment and spread probabilities. These results emphasize the importance of landscape-level characteristics as an essential component of invasion success.

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Author contributions

T.M-J, L.M. and E.V. designed the models and experiments, T.M-J performed the simulations, T.M-J and M.H. carried out the experiments and data analyses, all authors participated in the writing of the manuscript.

Competing financial interests

The authors declare no competing financial interests.

Data availability

The computer code to perform the simulations and the experimental data will be made available on Dryad upon acceptance.

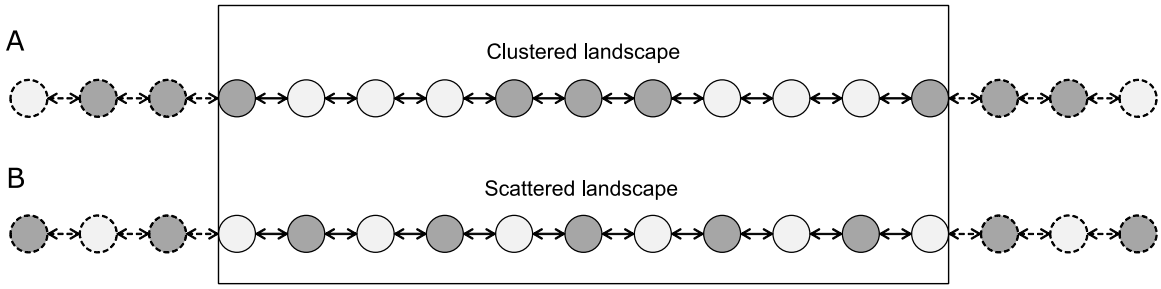

Figure 1: Schematic representation of the landscapes considered (A, B), and the way patches were connected in the experiment (C, D, E). Patches are represented as circles, and arrows as possible dispersal paths. The clustered (A) and scattered landscapes (B) are a part of an infinite landscape with alternating good patches (dark grey circles) and bad patches (light grey circles). Each landscape is made up of 11 patches (in the box). In the experiment, two corridors linked neighbouring patches, with no (C), one (D) or two dead-ends (D) for low, medium and high dispersal mortality respectively.

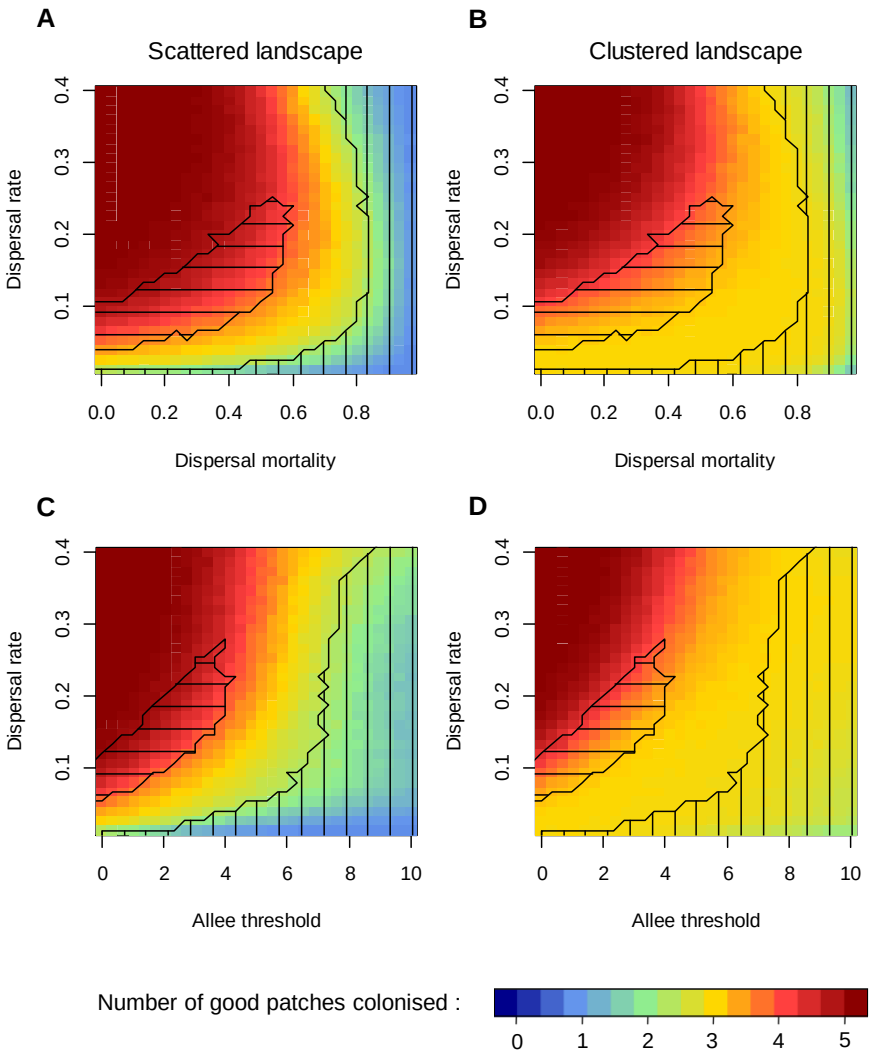

Figure 2: Mean maximal number of good patches colonised (from dark blue to dark red), ten generations after introduction over 1000 simulations, for different dispersal rates and dispersal mortality levels (A, B) or Allee thresholds (C,D), in scattered (A, C) and clustered landscape (B, D). Parameter combinations for which invasions in scattered landscapes colonised on average at least 0.5 more patches than in clustered landscapes are hatched horizontally. Parameter combinations for which invasions in clustered landscapes colonised on average at least 0.5 more patches than in scattered landscapes are hatched vertically.

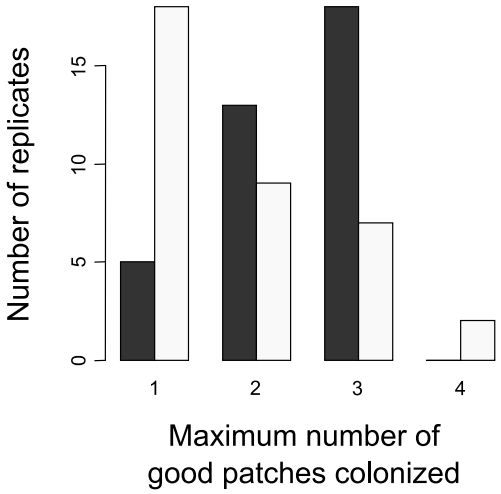

Figure 3: Maximum extent of the colonisation over the course of the experiment, as the number of good patches colonised, in the clustered landscape (dark bars) and the scattered landscape (light bars).

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